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Seed Rain and Seed Bank of Third- and Fifth-Order Streams on the Western Slope of the Cascade Range

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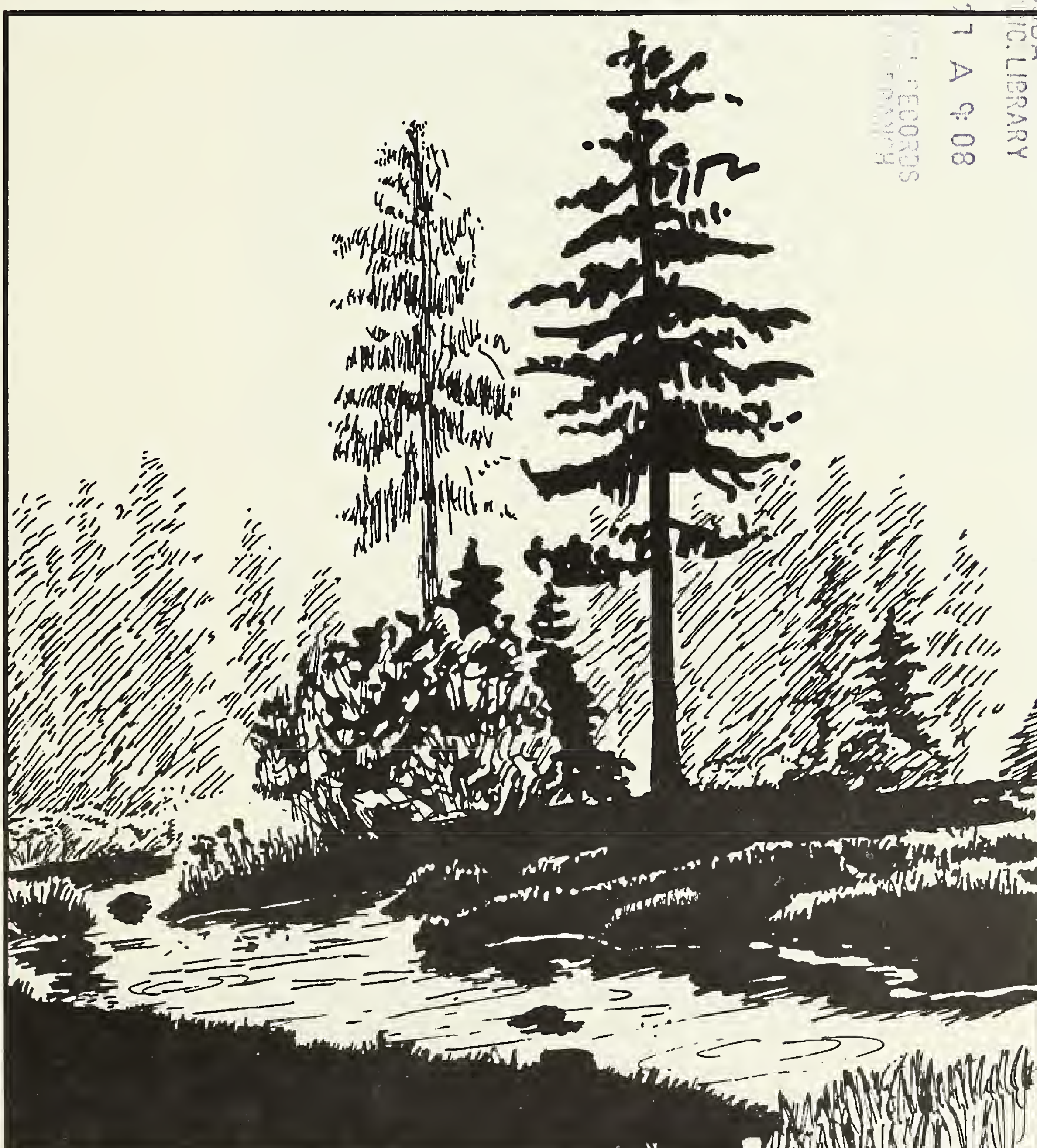

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Abstract

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We compared the composition and density of the on-site vegetation, seed bank, and seed rain of three geomorphic and successional surfaces along third- and fifth-order streams on the western slope of the central Cascade Range in Oregon.

The on-site vegetation generally was dominated by tree species, the seed bank by herb species, and the seed rain by tree and herb species. Seed rain density generally corresponded to the successional stage of the geomorphic surface and frequency of site disturbance, with the youngest and least vegetatively stable geomorphic surfaces having the highest density of trapped viable seeds. The highest density and greatest species richness of seed bank germinants were found on the intermediate-aged geomorphic surfaces, which had moderate levels of disturbance. In comparison, the younger and older geomorphic surfaces (with greater and lesser disturbance levels than the intermediate-aged surfaces, respectively) had equal but lower seed bank densities. The seed banks of the youngest, least stable geomorphic surfaces, however, were substantially richer in species than those of the oldest, most vegetatively stable surfaces.

A large and diverse array of plant propagules, provided by both seed rain and seed banks, are available to riparian sites in forests in the Pacific Northwest. Many of the propagules represent species currently absent from the aboveground vegetation on these sites.

Keywords: Disturbance, riparian zones, seed bank, seed rain, species richness.

Summary

The purpose of this study was to gather baseline data on the natural ability of riparian habitats to revegetate after a disturbance. To do this, we compared the composition and density of the on-site vegetation, seed bank, and seed rain of three geomorphic and successional surfaces along third- and fifth-order streams on the western slope of the central Cascade Range in Oregon. The timeframe for the project encompassed 1 year, with seed rain sampling basically occurring monthly and on-site vegetation and seed bank samples obtained and recorded once. The sample sites were two third-order and two fifth-order stream locations, which were fairly representative of these size streams at the H.J. Andrews Experimental Forest. On-site vegetation was dominated by tree species, seed bank by herb species, and seed rain by both tree and herb species. Highest density of trapped seed rain species occurred on the least stable geomorphic surfaces. Highest density and greatest species richness for the seed bank germinants occurred on the intermediately disturbed geomorphic surfaces. Many seed bank species were absent from the community of on-site vegetation.

Introduction

Much of our understanding of seed banks, buried seed communities, comes from studies of terrestrial environments (Leck and Graveline 1979). Particularly, the seed bank composition of many forests in North America has been compared to the on-site vegetation (Graber and Thompson 1978, Kellman 1974, Koniak and Everett 1982, Livingston and Allessio 1968, Oosting and Humphreys 1940, Pratt and others 1984, Quick 1956, Strickler and Edgerton 1976, Thompson 1978, Whipple 1978). Two trends emerge: first, seed banks of mature forests tend to be more species rich than the existing vegetation; and second, densities of buried viable seeds decline with the successional age of a forest.

Studies of seed banks also have been conducted for freshwater wetland habitats (Keddy and Reznicek 1982; Leck and Graveline 1979; Parker and Leck 1985; Smith and Kadlec 1983, 1985; Van Der Valk and Davis 1978, 1979). In some of these studies, the seed banks and on-site vegetation had similar species compositions (Leck and Graveline 1979, Van Der Valk and Davis 1978); however, in other studies, they did not (Smith and Kadlec 1983, Thompson and Grime 1979). Plant succession in wetlands is controlled by many environmental factors. Water level conditions during germination, past seed input, presence of existing vegetation, salinity levels, and disturbance of the substrate surface are some of the factors thought to affect germination and growth of wetland seed bank species (Smith and Kadlec 1983).

Little research has been conducted on either the seed bank or the seed rain, seed input, of riparian zones. Possibly, this is because riparian zones frequently are severely disturbed by flooding, and, as with our study sites, they represent narrow interruptions in forest cover. These characteristics, however, do not diminish the ecological importance of these zones. Riparian zones are distinctive as interfaces between two markedly different environments—aquatic and terrestrial (Swanson and others 1982). As such, riparian zones have sharp gradients of environmental factors and ecological processes. These gradients contribute to the diversity and the spatial and temporal heterogeneity of adjoining terrestrial and aquatic systems (Gregory and others 1991). With their unique physical characteristics, riparian zones clearly are an important habitat for the study of plant succession.

An understanding of plant reproductive strategies is important for any successional perspective. Because both seed rain and seed banks are sources of the potential population of a habitat (Harper 1977), they can play significant roles in initial successional processes. In this study, we compared the composition of the on-site vegetation, the seed bank, and the seed rain of three streamside surfaces with different geomorphic and successional characteristics. The overall objective of our study was to identify the potential contribution of seed rain and seed banks to the on-site vegetation in riparian zones.

Study Area

The H.J. Andrews Experimental Forest lies on the western slope of the Cascade Range, about 80 km east of Eugene, Oregon. This area supports dense forests of *Pseudotsuga menziesii* (Mirb.) Franco[1] (table 1) and *Tsuga heterophylla* (Raf.) Sarg. typical of northwestern Oregon and western Washington. Comprehensive sampling and classification of riparian vegetation in this area has been done by Campbell and Franklin (1979). For our study sites, we selected a total of four riparian sites. Two of the sites were located alongside two fifth-order streams, one site per stream, (for definition of stream order, see Strahler 1957), elevations ca. 460 m. The remaining two sites were located alongside one third-order stream, ca. 825 m in elevation. All the sites were relatively stable; floods in the preceding 10 years had not greatly altered their geomorphic surfaces or vegetative cover.

Three geomorphic surfaces, each with different vegetation, were sampled at each site: (1) flood plain with old-growth forest (OG), (2) vegetated gravel bars within the active stream channel (VGB), and (3) unvegetated gravel bars within the active stream channel (GB). At all sites, the OG surfaces no longer or only rarely were flooded. The VGB surfaces at the two third-order sites had flood recurrence intervals of from 2 to 100 or more years, but normally could be characterized by a 2- to 10-year flood recurrence interval. The VGB surfaces at the two fifth-order sites were flooded more frequently—every 1.25 to 5 years. The GB surfaces at all sites were flooded annually (table 2).

The climate of the study area is typical for the Pacific Northwest, with mild wet winters and warm dry summers. The precipitation averages 240 cm annually and is strongly seasonal, with most occurring between November and March. The 10-year average (1977-86) of mean yearly temperature for the third-order sites was 7.1 °C, with the average maximum of 21.4 °C occurring in July or August and the average minimum of -1.3 °C occurring in December or January. For the fifth-order sites, the corresponding 10-year average for mean yearly temperature was 8.7 °C, with the average maximum of 24.2 °C also occurring in July or August and the average minimum of -7.8 °C occurring in November, December, or January.[2]

At all study sites, the stream-bottom soils chiefly were colluvial and alluvial and were poorly developed (Swanson and James 1975). At the upper elevation, third-order sites (as typical for small third-order streams), soil creep and minor slides had combined with channel erosion to create narrow, V-shaped valley floors with steep stream gradients and no terraces. Soils were those of the surrounding upslope forest. At the lower, fifth-order sites, hill slopes graded abruptly to valley floor landforms of flood plains, alluvial fan deposits, and terraces.

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[1] Scientific nomenclature follows Hitchcock and Cronquist (1973).

[2] Weather data. On file with: Headquarters Office of the H.J. Andrews Experimental Forest, Box 300, Blue River, Oregon 97413.

Table 1—Species names

Scientific name	Common name
Trees:	
Acer macrophyllum	Big-leaf maple
Alnus rubra	Red alder
Cornus nuttallii	Pacific dogwood
Populus tricocarpa	Black cottonwood
Prunus emarginata	Bittercherry
Pseudotsuga menziesii	Douglas-fir
Thuja plicata	Western redcedar
Tsuga heterophylla	Western hemlock
Shrubs:	
Acer circinatum	Vine maple
Acer macrophyllum	Big-leaf maple
Berberis nervosa	Dull Oregongrape
Corylus cornuta	Hazelnut
Gaultheria shallon	Salal
Oplopanax horridum	Devil's club
Rhamnus purshiana	Cascara
Rhododendron macrophyllum	Pacific rhododendron
Ribes bracteosum	Stink currant
Rubus leucodermis	Black raspberry
Rubus nivalis	Snow bramble
Rubus parviflorus	Thimbleberry
Rubus spectabilis	Salmonberry
Rubus ursinus	Pacific blackberry
Salix sitchensis	Sitka willow
Sambucus cerulea	Blue elderberry
Taxus brevifolia	Western yew
Thuja plicata	Western redcedar
Tsuga heterophylla	Western hemlock
Vaccinium alaskaense	Alaska blueberry
Vaccinium membranaceum	Thin-leaved blueberry
Vaccinium parvifolium	Red blueberry
Herbs:	
Achlys triphylla	Vanillaleaf
Adenocaulon bicolor	Pathfinder
Anaphalis margaritacea	Common pearly-everlasting
Anemone deltoidea	Threeleaf anemone
Angelica arguta	Sharptooth angelica
Aralia californica	California aralia
Aruncus sylvester	Goatsbeard
Asarum caudatum	Wild ginger
Boykinia elata	Slender boykinia
Cardamine occidentalis	Western bittercress

Table 1–Species names (continued)

Scientific name	Common name
Cardamine oligosperma	Little western bittercress
Cerastium viscosum	Sticky chickweed
Chimaphila umbellata	Prince's-pine
Chrysanthemum leucanthemum	Oxeye-daisy
Circaea alpina	Enchanter's nightshade
Cirsium arvense var. *horridum*	Canada thistle
Cirsium vulgare	Common thistle
Clintonia uniflora	Queen's cup
Collomia heterophylla	Varied-leaf collomia
Conyza canadensis	Horseweed
Coptis laciniata	Cutleaf goldthread
Cornus canadensis	Bunchberry
Dicentra formosa	Pacific bleedingheart
Epilobium angustifolium	Fireweed
Epilobium glaberrimum var. *glaberrimum*	Smooth willow-herb
Epilobium glandulosum	Common willow-herb
Epilobium paniculatum	Autumn willow-herb
Epilobium watsonii	Watson's willow-herb
Galium triflorum	Sweetscented bedstraw
Gnaphalium microcephalum var. *thermale*	Slender cudweed
Goodyera oblongifolia	Western rattlesnake-plantain
Heracleum lanatum	Cow-parsnip
Hydrophyllum tenuipes	Pacific waterleaf
Hypericum perforatum	Common St. John's-wort
Hypochaeris radicata	Spotted cats-ear
Lactuca muralis	Wall lettuce
Linnaea borealis var. *longiflora*	Western twinflower
Madia sp.	Tarweed
Microsteris gracilis var. *humilior*	Pink microsteris
Mimulus breweri	Brewer's monkey-flower
Mimulus guttatus	Yellow monkey-flower
Mimulus moschatus	Musk-flower
Mitella ovalis	Oval-leaved mitrewort
Montia parvifolia	Littleleaf montia
Montia sibirica	Western springbeauty
Nemophila parviflora var. *parviflora*	Small-flowered nemophila
Oenanthe sarmentosa	Pacific water-parsley
Osmorhiza chilensis	Sweet-root
Oxalis trilliifolia	Great oxalis
Petasites frigidus var. *palmatus*	Coltsfoot
Polygonum minimum	Broadleaf knotweed
Prunella vulgaris	Self-heal

Table 1–Species names (continued)

Scientific name	Common name
Pyrola asarifolia	Pyrola
Ranunculus uncinatus	Little buttercup
Rumex obtusifolius	Bitterdock
Saxifragaceae	Saxifrage family
Senecio sylvaticus	Wood groundsel
Senecio triangularis	Arrowleaf groundsel
Smilacina stellata	Starry Solomon-plume
Stachys cooleyae	Cooley's hedge-nettle
Stachys rigida	Rigid hedge-nettle
Stellaria crispa	Crisped starwort
Stellaria longifolia	Longleaved starwort
Streptopus amplexifolius	Clasping-leaved twisted-stalk
Taraxacum officinale	Common dandelion
Tellima grandiflora	Fringecup
Thalictrum occidentale	Western meadowrue
Tiarella trifoliata var. *unifoliata*	Coolwort foamflower
Tolmiea menziesii	Pig-a-back-plant
Trifolium repens	White clover
Trifolium subterraneum	Subterraneum clover
Trillium ovatum	White trillium
Umbelliferae sp.	Parsely family
Vancouveria hexandra	Inside-out-flower
Veronica americana	American brooklime
Viola glabella	Stream violet
Viola orbiculata	Round-leaved violet
Viola sempervirens	Redwoods violet
Grasses:	
Agrostis alba	Redtop
Agrostis exarata var. *exarata*	Spike bentgrass
Agrostis exarata var. *monolepis*	Spike bentgrass
Agrostis oregonensis	Oregon bentgrass
Cinna latifolia	Woodreed
Deschampsia elongata	Slender hairgrass
Elymus glaucus var. *jepsonii*	Blue wildrye
Festuca subulata	Bearded fescue
Poa trivialis	Roughstalk bluegrass
Poa palustris	Fowl bluegrass
Trisetum canescens	Tall trisetum
Sedges and rushes:	
Carex amplifolia	Big-leaf sedge
Carex deweyana	Dewey's sedge
Carex fracta	Fragile-sheathed sedge
Carex microptera	Small-winged sedge
Juncus effusus	Soft rush
Juncus ensifolius	Daggerleaf rush
Luzula parviflora	Smallflowered woodrush

Table 2—Site characteristics

Site	Stream order	Elevation	Geomorphic surface[a]	Flood recurrence interval
		Meters		*Years*
1	3d	About 825	OG VGB GB	>100 2–>100 Annually
2	3d	About 825	OG VGB GB	>100 5–10 Annually
3	5th	About 460	OG VGB GB	>100 5 Annually
4	5th	About 460	OG VGB GB	>100 1.25 yr Annually

[a] OG = flood plain with old-growth forest, VGB = vegetated gravel bar, and GB = bare gravel bar.

Field and Greenhouse Methods

Vegetation cover—Plant cover by species was estimated at each site during the latter part of June 1986. Percentage of cover was estimated for herb and shrub species within 1 m of each seed rain trap (see the next section). Presence of flowers and seeds for the herb and shrub species also was recorded. Overstory cover was estimated by eye roughly within sight of each seed trap to include potential contributors of wind-dispersed seeds. Tree species were assigned general cover classifications of "dominant" (50-100 percent), "codominant" (30-50 percent), "common" (10-30 percent), and "occasional" (1-10 percent).

Seed rain—In early June 1986, 20 seed traps were placed randomly along a transect on the three surfaces of each study site for a total of 60 seed traps per site. Some of the VGB and GB surfaces at the selected sites were too small to hold all 20 traps; in these situations, one or more similar surfaces downstream also were used for trap placement. At all sites, the stretch of stream sampled was about 100 m. The seed traps consisted of circular plastic containers with a top diameter of 11 cm and a depth of about 8 cm, with holes drilled in the bottom for water drainage. Seed trap liners made of 0.10-mm mesh netting were placed inside the containers and secured with plastic rims. A 16-penny nail and metal washer inserted through the bottom of each container anchored the traps to the sites. During mid-June 1986, bailing twine coated with Tanglefoot[3] was wrapped around the containers to reduce seed predation by ants. Seed trap liners were collected monthly for 1 year. Seeds were separated from other litter, identified, counted, and cut to check the endosperm to test for viability (USDA Forest Service 1974).

[3] The use of trade, firm, or corporation names in this publication is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the U.S. Department of Agriculture of any product or service to the exclusion of others that may be suitable.

Seed bank—Seed bank studies were based on 20 soil samples collected from each of the 3 geomorphic surfaces at each study site. The soil samples were 15 by 15 by 5 cm and were taken 1 m from the corresponding seed trap location (On the GB surfaces, the sample surface area was enlarged as necessary to compensate for large rocks that interfered with soil extraction). Samples were collected soon after snowmelt in 1987 (mid-March for the fifth-order sites and early April for the third-order sites) and stored in individual plastic bags at 1.1 °C—the fifth-order samples for 4 days and the third-order samples for 2 days.

After cold storage, all roots and rhizomes were removed from the soil samples, and the samples were assigned randomly to plastic germination trays in a greenhouse whose maximum and minimum temperatures (recorded biweekly) averaged 29.7 and 10.4 °C, respectively. The germination trays were 43 by 40 by 6 cm and were divided in half with a stiff piece of plastic so they could hold two samples each. The trays were filled with a mixture of sterilized sand and vermiculite to a depth of 4 cm; the soil samples were spread over this mixture to a depth of about 1 cm. A control tray was located randomly on each greenhouse table, for a total of six control trays. At each observation time (about every 1 to 2 weeks), the new germinants were marked with a plastic toothpick of a designated color. After the germinants were identified, they were pulled or cut. Plants that germinated in the control trays were considered invader species and were pulled from the sample trays. Peters professional brand 20-20-20 fertilizer was applied about once a month; Vapona spray was used as needed to eliminate fungus gnats. The soil samples were discarded in early October 1987. Unknown species were retained in the trays and placed outdoors in cold frames for later identification.

Flood Recurrence Interval

To determine the geomorphic surface elevations and the streambed widths and slopes at each study site, stream cross sections were measured in November 1987. The cross-section measurements were made with staff-and-rod readings taken perpendicularly to the axis of each stream and in about 1-m increments or at a change in slope. Then streambed particle size was measured at either 50 or 100 locations (depending on stream size) along the study site reaches by using Wolman's (1953) method. To calculate the discharge required to flood each of the geomorphic surfaces, the stream cross-section and particle-size data were analyzed with a cross-sectional analysis program (Grant 1987). To estimate the recurrence intervals for these calculated discharges, we used flow records from the United States Geological Survey (USGS) gauging station at Lookout Creek (Friday and Miller 1984).

Analytical Methods

The experimental design for the analysis of variance was a split plot, with stream order as the main plot treatment and geomorphic surface as the subplot treatment. Detrended correspondence analysis (Hill 1979) was used to ordinate a combined data set of the on-site vegetation, seed rain, and seed bank data. Rare species were downweighted. The combined data set analysis used relative cover for the on-site vegetation data, relative density of viable seeds for the seed rain data, and relative density of germinants for the seed bank data.

Results

Vegetation

At our study sites, tree cover dominated the geomorphic surfaces, but understory vegetation differed markedly among the three types of surfaces. Between the third- and fifth-order sites, vegetation differences corresponded to differences in elevation.

Dominant overstory vegetation was similar at both the third- and fifth-order OG surfaces (table 3). *Pseudotsuga menziesii, Tsuga heterophylla*, and *Thuja plicata* Donn. were the dominant tree species, although *Thuja* was much more common at the higher elevation (third-order) sites. The VGB surfaces were dominated by *Alnus rubra* Bong. at fifth-order sites and by conifers and *Acer macrophyllum* Pursh at third-order sites. The overstory cover for the GB surfaces was rooted on the adjacent vegetated surfaces.

Understory composition of the OG surfaces generally reflected elevational differences (table 3). The lower and warmer fifth-order sites were characterized by *Acer circinatum* Pursh, *Berberis nervosa* Pursh, *Corylus cornuta* Marsh., *Gaultheria shallon* Pursh, *Oxalis oregana* Nutt., and *Linnaea borealis* L. This community is comparable to the *Tsuga heterophylla/Rhododendron macrophyllum* G. Don-*Berberis nervosa* association of Dyrness and others (1974) and Hemstrom and others (1987). The higher and cooler third-order sites were dominated by *Acer circinatum, Rhododendron macrophyllum, Vaccinium alaskaense* Howell, and *Cornus canadensis* L. This community is related to the *Abies amabilis* (Dougl.) Forbes/*Rhododendron macrophyllum-Vaccinium membranaceum* Dougl. association of Dyrness and others (1974) and Hemstrom and others (1987).

On the VGB surfaces, understories differed substantially among stream orders (table 3). Shrubs such as *Ribes bracteosum* Dougl., *Oplopanax horridum* (Smith) Miq., and *Rubus spectabilis* Pursh dominated at the third-order sites; herbs such as *Tiarella trifoliata* L. provided only modest cover. However, on the fifth-order sites, where understories were shaded heavily for much of the growing season by dense *Alnus rubra,* herbs dominated. *Tolmiea menziesii* (Pursh) T. & G. was the most abundant herb, but many other species exhibited cover values of >1 percent (for example, *Heracleum lanatum* Michx., *Petasites frigidus* var. *palmatus* (Ait.) Cronq., *Montia sibirica* (L.) Howell, *Lactuca muralis* (L.) Fresen., *Aralia californica* Wats., *Circaea alpina* L., and *Stachys cooleyae* Heller).

The GB surfaces were sparsely vegetated by herb and shrub species (table 3). At third-order sites, these surfaces were small and typically isolated from each other, and the vegetative cover was comparable to individual communities described by Campbell and Franklin (1979). At fifth-order sites, herb and shrub cover was sparse. *Salix sitchensis* Sanson was the only rooted shrub, and *Petasites* was the only herb.

Seed Rain

The mean yearly total of trapped viable seeds per m^2 generally increased from the OG surfaces out to the GB surfaces (table 4), averaging 527 for OG surfaces, 1,075 for VGB surfaces, and 2,084 for GB surfaces. The number of trapped viable seeds, however, was not significantly different between either stream order or geomorphic surface; the interaction of these two variables was not significant. Shrub seed fall on the third-order sites was extremely low.

Seed rain species richness, on the other hand, differed significantly by both geomorphic surface and stream order. Generally, seed rain species richness was greatest on the surfaces within the active stream channel. Many fewer species were captured in the seed traps (table 5), however, than were present either in the on-site vegetation (table 3) or in the seed bank (table 6).

Text continues on page 18.

Table 3—On-site vegetative cover

Growth-form species	Geomorphic surface and stream order					
	Old growth		Vegetated gravel bar		Gravel bar	
	3d	5th	3d	5th	3d	5th
	Percent mean cover per m^2					
Trees:[a]						
Acer *macrophyllum*	0	Occasional	Common	0	Codominant	Occasional
Alnus rubra	0	0	0	Dominant	0	Dominant
Cornus nutallii	0	Occasional	0	0	0	0
Pseudotsuga menziesii	Codominant	Codominant	Common	0	Codominant	Occasional
Thuja plicata	Codominant	Occasional	Codominant	Occasional	Codominant	Occasional
Tsuga heterophylla	Codominant	Codominant	Codominant	Occasional	Codominant	0
Total, percentage of mean tree cover per m^2	55.4	50.3	48.3	67.1	76.4	93.4
Shrubs:						
Acer circinatum	12.1	29.7	6.81	0	9.2	0
Acer macrophyllum	0	0	0	1.1	0	0
Berberis nervosa	0	14.7	0	0	0	0
Corylus cornuta	0	7.3	0	0	0	0
Gaultheria shallon	0	3.7	0	0	0	0
Oplopanax horridum	0	0	22.6	0	1.1	0
Rhamnus purshiana	0	0	0	0	0	2.5
Rhododendron macrophyllum	0	9.3	0	0	0	0
Ribes bracteosum	0	0	48.6	.3	3.4	0
Rubus nivalis	.4	0	0	0	0	0
Rubus parviflorus	0	0	0	T[b]	0	0
Rubus spectabilis	.1	.4	10.7	2.2	2.1	0
Rubus ursinus/R. leucodermis	1.4	2.9	0	.6	0	0
Salix sitchensis	0	0	0	0.1	0	1.8
Taxus brevifolia	.1	0	.1	0	0	T
Thuja plicata	1.6	0	0	T	0	0
Tsuga heterophylla	9.7	0	T	0	T	0
Vaccinium alaskaense	11.0	0	T	0	T	0
Vaccinium membranaceum	.1	0	0	0	0	0
Vaccinium parvifolium	9.1	4.6	T	0	.9	.8
Total, percentage of mean shrub cover per m^2	30.6	31.2	45.1	3.0	13.2	6.1

Table 3–On-site vegetative cover (continued)

	Geomorphic surface and stream order					
	Old growth		Vegetated gravel bar		Gravel bar	
Growth-form species	3d	5th	3d	5th	3d	5th
	Percent mean cover per m^2					
Herbs:						
Achlys triphylla	.4	0	0	0	0	0
Adenocaulon bicolor	0	.1	T	.3	0	0
Anemone deltoidea	.1	0	0	0	T	0
Aralia californica	0	0	0	1.8	0	0
Aruncus sylvester	0	0	0	0	1.6	0
Asarum caudatum	t	0	.4	0	0	0
Boykinia elata	0	0	0	0	.2	0
Chimaphila umbellata	.1	.3	0	0	0	0
Circaea alpina	0	0	.2	1.6	.3	0
Clintonia uniflora	2.9	1.5	0	0	0	0
Coptis laciniata	0	.5	0	0	0	0
Cornus canadensis	9.4	0	.2	0	0	0
Dicentra formosa	0	0	.1	.3	0	0
Epilobium glandulosum	.1	0	0	0	0	0
Galium triflorum	0	0	1.0	1.4	1.0	0
Goodyera oblongifolia	.5	0	0	0	0	0
Heracleum lanatum	0	0	0	5.3	0	0
Hydrophyllum tenuipes	0	0	1.0	.4	.9	0
Lactuca muralis	0	0	0	2.1	0	0
Linnaea borealis var. *longiflora*	3.9	13.3	0	0	0	0
Mimulus guttatus	0	0	0	.5	0	0
Mitella ovalis	0	0	1.2	0	.4	0
Montia parvifolia	0	0	0	.4	1.5	0
Montia sibirica	0	0	.1	2.8	.3	0
Nemophila parviflora var. *parviflora*	0	0	0	1.3	0	0
Osmorhiza chilensis	0	0	0	1.1	0	0
Oxalis oregana	0	16.3	.2	3.8	.4	0
Oxalis trilliifolia	0	0	1.4	0	.6	0
Petasites frigidus var. *palmatus*	0	0	0	4.5	.5	1.2
Prunella vulgaris	0	0	0	1.0	0	0
Pyrola asarifolia	.1	0	0	0	0	0
Ranunculus uncinatus	0	0	0	.2	0	0
Rumex obtusifolius	0	0	0	.6	0	0

Table 3—On-site vegetative cover (continued)

	Geomorphic surface and stream order					
	Old growth		Vegetated gravel bar		Gravel bar	
Growth-form species	3d	5th	3d	5th	3d	5th
			Percent mean cover per m²			
Smilacina stellata	4.4	0	.2	0	0	0
Stachys cooleyae	0	0	.4	1.5	1.5	0
Streptopus amplexifolius	0	0	.1	0	T	0
Thalictrum occidentale	0	0	0	.6	0	0
Tiarella trifoliata var. *unifoliata*	2.7	1.5	4.6	.2	.4	0
Tolmiea menziesii	0	0	.1	8.7	1.3	0
Trillium ovatum	.3	1.0	.2	0	0	0
Vancouveria hexandra	.3	2.8	.1	.3	0	0
Viola glabella	.3	0	0	0	0	0
Viola sempervirens	.3	T	.1	0	.3	0
Total, percentage of mean herb cover per m^2	14.1	18.7	6.3	27.1	9.3	1.1
Grasses:						
Argrostis sp.	0	0	0	.4	.1	0
Festuca subulata	0	0	0	2.1	.9	0
Unknown grasses[c]	0	0	.4	0	.4	0
Sedges:						
Carex amplifolia	0	0	0	.4	0	0
Carex deweyana	0	0	T	1.3	0	0
Carex sp.	0	0	.1	0	0	0
Total, percentage of mean grass and sedge cover per m^2	0	0	.3	2.9	1.3	0

[a] Tree cover classifications are defined in the "Vegetation Cover" section of "Field and Greenhouse Methods" in this paper.

[b] T = trace amounts.

[c] There were 4 unknown grasses that were combined for these totals. In all other analyses, they were treated as individual species.

Table 4—Mean monthly number of viable trapped seeds per m^2

Site	Stream order	Geomorphic surface[a]	N[b]	Number of species	Minimum	Maximum	Mean	Standard deviation	Mean yearly total
1	3d	OG	33	9	0	79	12	20	382
		VGB	39	11	0	105	11	21	410
		GB	25	10	0	63	13	19	316
2	3d	OG	30	7	0	279	33	87	979
		VGB	44	17	0	447	35	87	1,528
		GB	22	10	0	2,211	173	475	3,798
3	5th	0G	37	10	0	126	10	22	351
		VGB	58	17	0	620	22	84	1,282
		GB	27	11	0	2,605	127	502	3,439
4	5th	OG	29	9	0	342	14	63	397
		VGB	54	18	0	211	20	45	1,080
		GB	31	14	0	467	25	84	783

[a] OG = flood plain with old-growth forest, VGB = vegetated gravel bar, and GB = bare gravel bar.

[b] N = number of seed traps. N varied due to temporary loss of some seed traps from flooding and coverage by snow.

Table 5—Number of viable trapped seeds per m^2

	Geomorphic surface and stream order					
	Old growth		Vegetated gravel bar		Gravel bar	
Growth-form species	3d	5th	3d	5th	3d	5th
Trees:						
Alnus rubra	0	0	0	155.3	0	36.8
Populus trichocarpa	0	0	0	5.8	0	5.8
Pseudotsuga menziesii	0	0	0	0	0	2.6
Thuja plicata	436.8	2.6	624.7	34.2	713.2	7.9
Tsuga heterophylla	121.1	65.8	126.9	7.9	102.1	7.9
Total, number of tree seeds per m^2	557.9	68.4	751.6	203.2	815.3	61.0
Shrubs:						
Oplopanax horridum	0	0	2.6	0	0	0
Salix sitchensis	0	0	0	0	0	233.7
Total, number of shrub seeds per m^2	0	0	2.6	0	0	0
Herbs:						
Boykinia elata	0	0	15.8	0	0	0
Circaea alpina	0	0	0	55.3	0	2.6
Epilobium angustifolium	81.6	250.0	63.2	107.9	51.6	281.6
Epilobium watsonii	0	0	0	0	0	1,302.6
Galium triflorum	0	0	0	0	0	2.6
Lactuca muralis	0	2.6	0	42.1	0	15.8
Linnaea borealis var. *longiflora*	0	5.3	0	2.6	3.2	0
Montia parvifolia	0	0	0	0	2.6	0
Montia sibirica	0	0	2.6	111.1	5.3	5.8

Table 5—Number of viable trapped seeds per m^2 (continued)

Growth-form species	Geomorphic surface and stream order					
	Old growth		Vegetated gravel bar		Gravel bar	
	3d	5th	3d	5th	3d	5th
Ranunculus uncinatus	0	0	0	37.4	0	0
Senecio sylvaticus	29.0	0	21.1	0	32.1	31.8
Tiarella trifoliata var. *unifoliata*	5.3	2.6	0	0	0	0
Tolmaie menziesii	0	10.5	0	417.4	34.2	107.9
Unknown dicots[a]	7.9	0	107.9	10.5	10.5	66
Total, number of herb seeds per m^2	123.8	271.0	210.6	784.3	139.5	1,817.5
Grasses:						
Argrostis sp.	0	0	2.6	5.3	1,110.5	0
Festuca subulata	0	0	0	107.9	0	0
Unknown grasses[b]	0	0	2.6	81.6	2.6	2.6
Total, number of grass seed per m^2	0	0	5.2	194.8	1,113.1	2.6
Sedges:						
Carex sp.	0	0	0	3.2	0	0
Total, number of sedge seeds per m^2	0	0	0	3.2	0	0

[a] There were 18 unknown dicot species that were combined for these totals. In all other analyses, they were treated as individual species.

[b] There were 4 species of grasses that were combined for these totals. In all other analyses, they were treated as individual species.

Table 6—Mean number of greenhouse germinants per m^2

Growth-form species	Geomorphic surface and stream order					
	Old growth		Vegetated gravel bar		Gravel bar	
	3d	5th	3d	5th	3d	5th
Trees:						
Alnus rubra	0	0	1	26	.5	2
Cornus nuttallii	1	0	0	0	0	0
Prunus emarginata	1	1	0	0	0	0
Pseudotsuga menziesii	1	2	1	0	.5	.5
Thuja plicata	9	0	2	0	2.5	0
Tsuga heterophyllo	0	0	0	1	3	T[a]
Total, mean tree germinants per m^2	12.0	3.0	4.0	27.0	6.5	2.5+
Shrubs:						
Acer circinatum	0	0	0	1	3	1
Gaultheria shallon	8	8	4.5	6.5	0	.5
Oplopanax horridum	0	0	2	0	0	0
Ribes bracteosum	0	0	24.5	0	2.5	.5
Ribes sp.	0	0	0	1	0	0
Rubus leuocodermis	0	51	5.5	4.5	.5	T
Rubus parviflorus	0	0	3	2	1	0
Rubus spectabilis	3.5	0	17.5	1	7.5	.5
Rubus ursinus	1	1	4	1	0	T
Rubus sp.	0	0	1	0	0	0
Sambucus cerulea	0	0	6.5	2	1	0
Vaccinium parvifolium	31	0	6.5	0	0	0
Total, mean shrub germinants per m^2	43.5	60.0	75.0	94.0	15.5	2.5+
Herbs:						
Anaphalis margaritacea	2	1	14.5	16	1	.5
Angelica arguta	0	0	0	0	1	0
Aralia californica	0	0	0	2	0	3
Aruncus sylvester	0	0	70	8	3	T
Asarum caudatum	0	0	1	0	0	0
Boykinia elata	1	0	155.5	181.5	34	34
Cardamine occidentalis	0	0	1	3.5	.5	0
Cardamine oligosperma	0	0	0	2	0	3
Cerastium viscosum	0	0	0	3.5	0	0
Chimaphila umbellata	0	0	1	0	0	0
Chrysanthemum leucanthemum	0	0	0	20.5	0	2
Circaea alpina	0	0	11	66.5	0	0

Table 6—Mean number of greenhouse germinants per m^2 (continued)

	Geomorphic surface and stream order					
	Old growth		Vegetated gravel bar		Gravel bar	
Growth-form species	3d	5th	3d	5th	3d	5th
Cirsium arvense var. *horridum*	0	2	1	0	.5	0
Cirsium vulgare	0	2	0	2	1	0
Collomia heterophylla	0	2	0	6.5	0	3.5
Conyza canadensis	0	1	1	7.5	.5	2
Cornus canadensis	10	0	0	0	0	0
Epilobium angustifolium	4.5	29	6.5	2	.5	.5
Epilobium glaberrimum var. *glaberrimum*	0	0	1	0	0	0
Epilobium paniculatum	1	1	0	0	0	0
Epilobium watsonii	34.5	56	80	88.5	35.5	17.5
Galium triflorum	0	0	36	36.5	3.5	.5
Gnaphalium microcephalum var. *thermale*	0	10	0	3	0	T
Heracleum lanatum	0	0	0	2.5	0	0
Hydrophyllum tenuipes	0	0	13.5	1	7.5	0
Hypericum perforatum	0	0	1	22.5	0	2
Hypochaeris radicata	0	1	0	0	0	0
Lactuca muralis	0	0	2	38.5	2	2
Linnaea borealis var. *longiflora*	2	3	0	0	0	0
Madia sp.	0	0	0	1	0	0
Microsteris gracilis var. *humilior*	0	0	0	0	0	.5
Mimulus breweri	0	0	7.5	0	.5	0
Mimulus guttatus	0	0	10	50.5	1.5	3.5
Mimulus moschatus	0	0	13	1	.5	0
Mitella ovalis	0	1	114.5	9	12	1
Montia parvifolia	0	0	1	11	2.5	T
Montia sibirica	0	0	0	65.5	5	2
Nemophila parviflora var. *parviflora*	0	0	0	7	0	0
Oenanthe sarmentosa	0	0	0	1	0	0
Oxalis trilliifolia	1	0	16	3	22.5	T
Petasites frigidus var. *palmatus*	0	0	0	1	0	.5
Polygonum minimum	0	0	0	0	0	2
Prunella vulgaris	0	0	0	2.5	0	0
Ranunculus uncinatus	0	0	3.5	7	0	0
Rumex obtusifolius	0	0	0	9	0	T

Table 6—Mean number of greenhouse germinants per m^2 (continued)

	Geomorphic surface and stream order					
	Old growth		Vegetated gravel bar		Gravel bar	
Growth-form species	3d	5th	3d	5th	3d	5th
Saxifragaceae sp.	0	0	4.5	1	1	0
Senecio sylvaticus	32	77.5	29	3	22	1
Senecio triangularis	0	0	1	0	0	0
Stachys cooleyae	0	0	4.5	3	2.5	.5
Stachys rigida	0	0	1	0	0	0
Stellaria crispa	0	0	5.5	41.5	3.5	0
Stellaria longifolia	0	0	0	9.5	0	T
Taraxacum officinale	0	0	0	0	1	0
Tellima grandiflora	0	0	0	1	1	0
Tiarella trifoliata var. *unifoliata*	12.5	0	7.5	0	0	0
Tolmiea menziesii	1	4.5	612	507	6.5	11
Trifolium repens	0	0	2	0	0	.5
Trifolium subterraneum	0	0	1	.5	0	0
Umbelliferae sp.	1	0	2	1	0	0
Vancouveria hexandra	0	2	0	0	0	0
Veronica americana	0	0	1	22	0	T
Veronica serpyllifolia	0	0	0	0	.5	0
Viola orbiculata	1	0	0	0	0	0
Unknown dicots[b]	1	2	37	87.5	6.5	4.5
Total, mean herb germinants per m^2	103.5	195.0	1,266.5	1,358.5	214.5	97.5+
Grasses:						
Agrostis alba	0	0	9	10.5	.5	T
Agrostis exarata var. *exarata*	0	0	8.5	112	.5	8
Agrostis exarata var. *monolepis*	0	0	0	1	0	1
Agrostis oregonensis	0	0	3.5	0	0	0
Agrostis sp.	3.5	0	5.5	9	1	1
Cinna latifolia	0	0	73.5	10	29.5	T
Deschampsia elongata	0	0	0	3	0	.5
Elymus glaucus var. *jepsonii*	0	0	0	4.5	0	T
Festuca subulata	0	0	0	4.5	1.5	0
Poa sp. (*trivialis* or *palustris*)	0	0	9	17	4.5	1.5
Trisetum canescens	0	0	0	1	1	0
Unknown grasses[c]	0	1	4.5	18.5	0	1.0
Total, mean grass germinants per m^2	3.5	1.0	113.5	191.0	38.5	13.0+

Table 6—Mean number of greenhouse germinants per m^2 (continued)

	Geomorphic surface and stream order					
	Old growth		Vegetated gravel bar		Gravel bar	
Growth-form species	3d	5th	3d	5th	3d	5th
Sedges and rushes:						
Carex amplifolia	0	0	18.5	2	6.5	.5
Carex deweyana	0	1	16.5	90	4.5	1
Carex fracta	0	0	3.5	2.3	0	0
Carex microptera	0	0	19.5	2.3	3	1
Carex sp.	0	0	0	5	0	T
Juncus effusus	0	0	0	125	1	7.5
Juncus ensifolius	0	1	6.5	22.5	0	3.5
Luzula parviflora	0	0	11	18.5	1.5	2.5
Unknown sedges[d]	2	0	0	1	1	0
Total, mean sedge and rush germinants per m^2	2	2	75.5	268.6	17.5	8.5+

[a] T = trace amounts.

[b] All unknown dicots were combined in this table. In all other analyses, they were treated as individual species.

[c] All unknown grasses were combined in this table. In all other analyses, they were treated as individual species.

[d] All unknown sedges and rushes were combined in this table. In all other analyses, they were treated as individual species.

Of all growth forms, the seed fall composition of herb species most closely reflected the herb species present on site. But several wind-dispersed herb species comprising a considerable portion of the seed rain (for example, *Epilobium angustifolium* L., *Senecio sylvaticus* L., and *Lactuca muralis*) were absent from the on-site vegetation.

Seed Bank

Many viable seeds were found in the soil samples. A total of 4,394 seeds, representing 100 species, germinated during the greenhouse tests. The VGB surfaces had the highest mean number of germinants per m^2 (1,724) and the greatest species richness (table 7, figs. 1 and 2). The OG and GB surfaces had about equal mean numbers of germinants (218 and 222 per m^2, respectively), but the former were substantially less species rich. The GB surfaces at each site were similar in species richness to the corresponding VGB surfaces. Although the mean numbers of germinants were significantly different among geomorphic surfaces, the mean numbers of germinants were not significantly different between stream orders, and the interaction of the stream-order and geomorphic surface variables was not significant either.

Table 7—Mean number of seed bank germinants per m²

Site	Stream order	Geomorphic surface[a]	N[b]	Number of species	Minimum	Maximum	Mean	Standard deviation
1	3d	OG	20	14	0	489	207	135
		VGB	20	51	311	2,622	1,433	683
		GB	20	37	30	2,044	393	537
2	3d	OG	20	17	0	267	127	83
		VGB	20	46	133	4,578	1,658	1,095
		GB	20	41	10	775	224	231
3	5th	OG	20	16	0	711	238	187
		VGB	19	61	222	10,222	2,126	2,218
		GB	20	30	10	400	74	100
4	5th	OG	20	17	89	667	298	141
		VGB	20	61	0	4,756	1,678	1,422
		GB	22	53	20	622	198	193

[a] OG = flood plain with old-growth forest, VGB = vegetated gravel bar, and GB = bare gravel bar.
[b] N = number of soil samples.

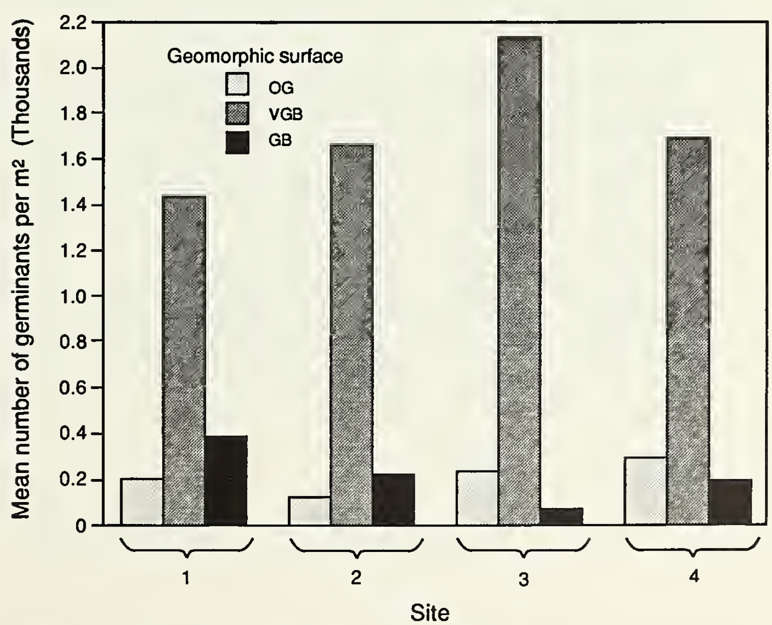

Figure 1—Mean number of seed bank germinants. Sites 1 and 2 are on third-order streams; sites 3 and 4 are on a fifth-order stream.

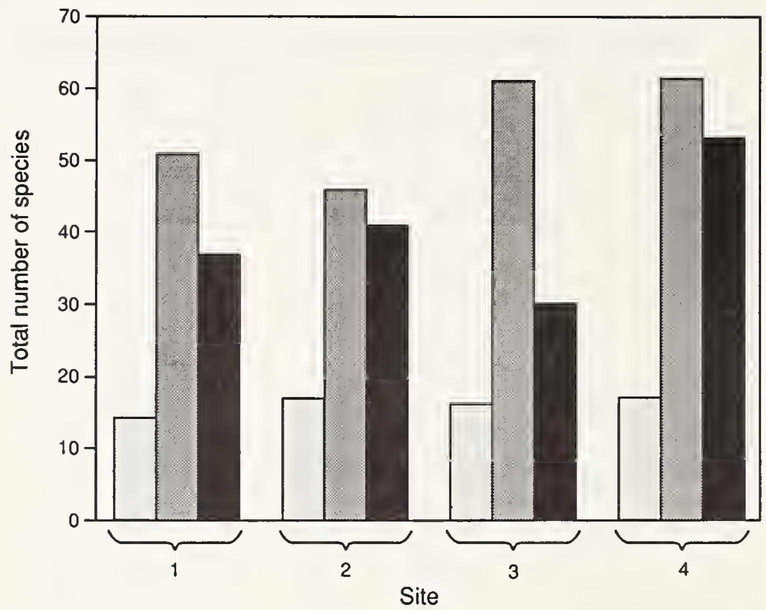

Figure 2—Total number of seed bank species. Sites 1 and 2 are on third-order streams; sites 3 and 4 are on a fifth-order stream.

The seed bank was dominated by herbaceous species (forbs and graminoids) (table 6). Dominant herb contributors were *Tolmiea menziesii*, *Boykinia elata* Nutt.) Greene, and *Epilobium watsonii* Barbey. The grasses *Agrostis exarata* var. *exarata* Trin. and *Cinna latifolia* (Trevir.) Griseb. also were abundant in the seed bank. Among the shrubs, *Rubus* spp. were the largest component of the seed bank; *Vaccinium parvifolium* Smith, *Gaultheria shallon*, and *Ribes bracteosum* also were common. Tree species were poorly represented.

Comparison of On-Site Vegetation, Seed Rain, and Seed Bank

In comparing the species composition of the on-site vegetation, the seed rain, and the seed bank at the four study sites, the seed bank and on-site vegetation showed the greatest difference from one another; seed rain occupied an intermediate position (fig. 3). The on-site vegetation was dominated by tree species (fig. 4), the seed rain by both tree and herb species (fig. 5), and the seed bank by herb species (fig. 6).

Many seed bank species were absent from the on-site vegetation of the community from which they were collected. For example, on average, only 23.4 percent of the seed bank herb species was present in the corresponding on-site vegetation. Seed bank shrub species averaged 32.5 percent in common with shrub species present in the on-site vegetation. With a mean of 62.5 percent, seed bank tree species had the most in common with the on-site vegetation.

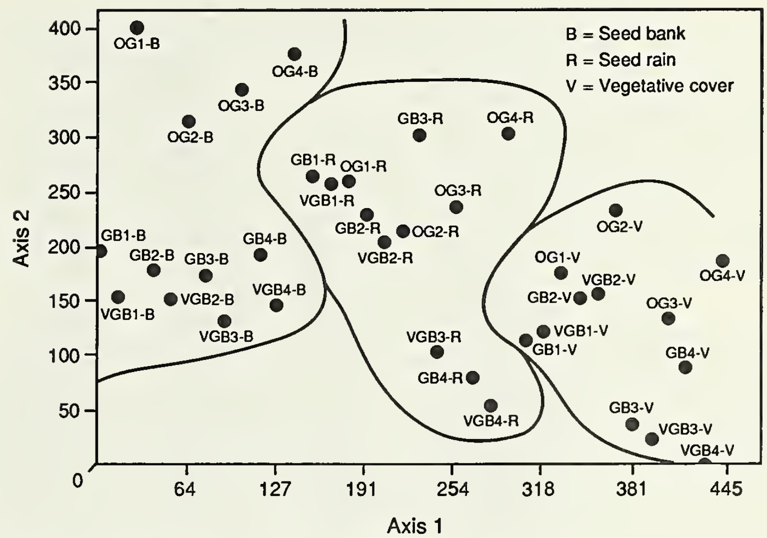

Figure 3—Ordination for combined data sets. Data points are identified by geomorphic surface type (OG, VGB, or GB), site number (1-4), and source (seed bank, seed rain, or cover vegetation). Rare species are downweighted.

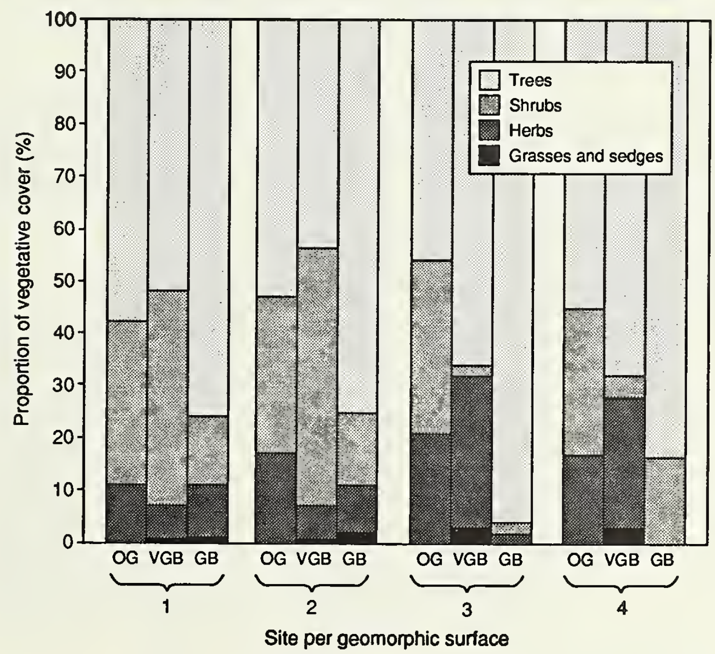

Figure 4—Growth forms of on-site vegetation.

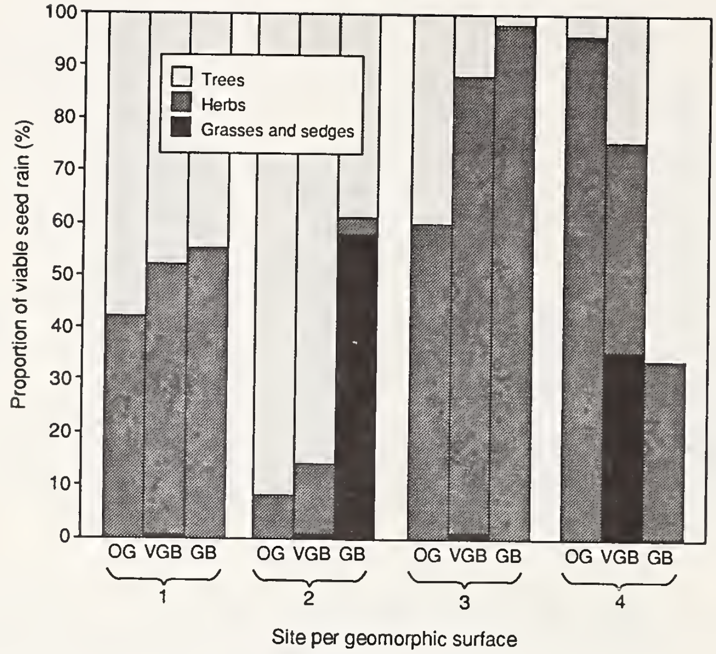

Figure 5—Growth forms of viable trapped seed rain. Shrub species contributed less than 0.12 percent to the seed rain and so are not represented in this figure.

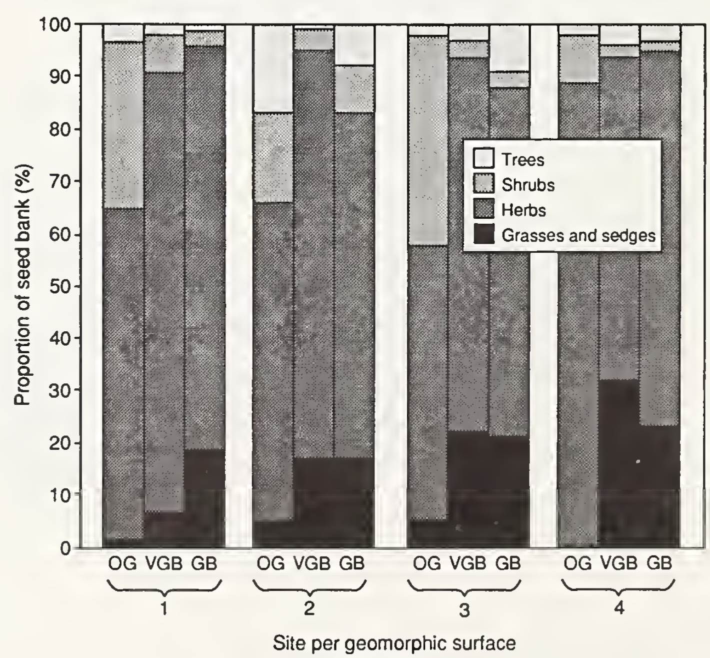

Figure 6—Growth forms of seed bank germinants.

Discussion

The availability of propagules is critical for the establishment of vegetation in any habitat. This study provides evidence that both seed rain and seed banks are important propagule sources in riparian communities. Although we did not evaluate vegetative propagation at our sites, Gecy (1988) found vegetative propagules important to early debris flow succession in first-order streams on the western slope of the Cascade Range. Quantitative data on the relative importance of imported vegetative material and on-site vegetative propagation in riparian plant establishment generally is lacking. Future studies in these areas would enhance our understanding of revegetation in riparian communities.

Seed rain was an important and continuing source of propagules on all the geomorphic surfaces studied. It should be noted, however, that our data only partially quantified this source for several reasons. First, there are serious technical difficulties in trapping seeds for an entire plant community (Rabinowitz and Rapp 1980). In our study, these difficulties included both the patchiness of seed rain (Archibold 1980, Harper 1977) and the trapping technique we used, which caught falling seeds but not seeds dispersed by water. Second, high yearly variability in seed production of many woody plants could not be addressed in a study that spanned only 1 year. For example, during our study year, viable seed fall for all the coniferous tree species was very low due to a poor cone crop.[4 5] Seed production by *Alnus rubra* at our sites also was exceptionally low, cumulatively averaging only 155 per m^2 within the site and only 37 per m^2 just outside the alder stand. For comparison, cumulative *Alnus* seed production during a good seed year in a western Washington alder stand ranged from about 6,600 per m^2 within the stand to about 200 per m^2 100 m out from the stand edge (Lewis 1985). And finally, the number of viable shrub seeds trapped on the VGB surfaces also was below average. (The low count initially was thought to be due to problems with method; however, the trapping results were confirmed by a survey of the fruiting structures of *Ribes bracteosum* Dougl., *Oplopanax horridum* (Smith) Miq., and *Rubus spectabilis* Pursh within a 1-m^2 area surrounding each seed trap on the VGB surfaces at sites 1 and 2. The survey revealed both a patchy spatial distribution and a low percentage of viable seeds for these shrub species.) Many more years of seed fall observation would be necessary to accurately quantify seed rain for an entire community.

Riparian habitats receive seed input from both indigenous and exogenous sources (fig. 7). In this study, the seed rains for the GB and VGB surfaces were substantially more species rich than the seed rain for the adjacent OG surfaces, primarily because the gravel-bar seed rains obtained substantial input from vegetation of several seral classes growing on adjacent surfaces. The OG surfaces, on the other hand, obtained most of their seed rain from the indigenous vegetation. In addition, the seed rain of fifth-order surfaces was more species rich than that of the third-order surfaces. This reflects the fact that third-order GB and VGB surfaces represent narrow interruptions in the forest landscape, whereas the corresponding fifth-order surfaces comprise relatively wide breaks in the landscape. The windshed for fifth-order streams also is much greater than that for third-order streams.

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[4] Unpublished cone crop data. On file with: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Way, Corvallis, Oregon 97331.

[5] Personal communication. 1987. Sally Swetland, USDA Forest Service, Blue River Ranger District, Blue River, Oregon 97413.

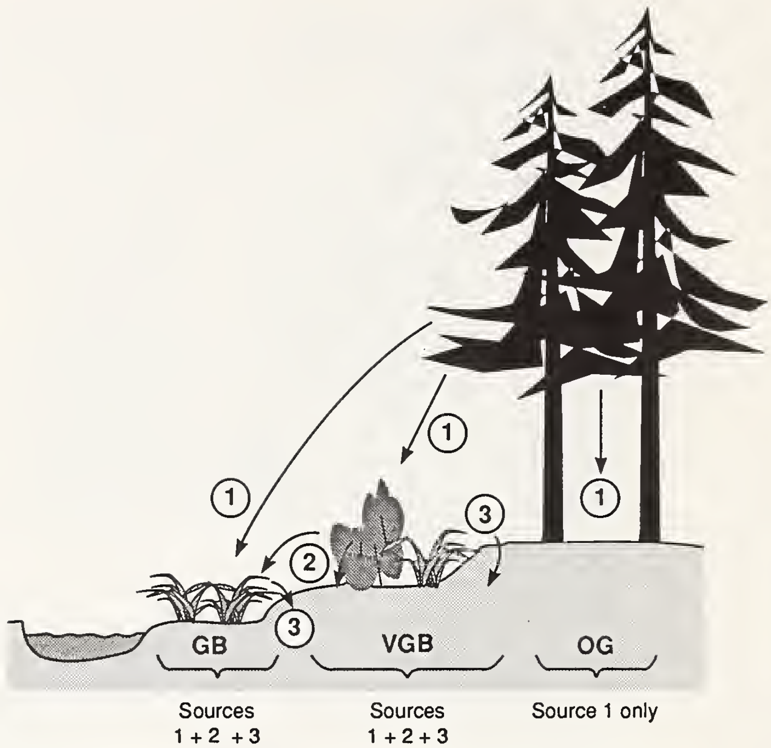

Figure 7—Hypothetical sources of seed rain.

Because seed banks represent both the accumulation and the survival of seed input, it is not surprising that the seed bank sizes and diversity in our study seemed related to the frequency of site disturbance by flooding. The disturbance frequency of the VGB surfaces was intermediate between that of the GB and OG surfaces. The VGB surfaces also had the greatest total number of germinants and the highest species richness. The erosive and depositional effects of periodic (but not annual) flooding combined to make the seed banks of the VGB surfaces highly diverse and potentially very productive. On the other hand, the yearly flooding of the GB surfaces (surfaces that represent an early successional stage) severely affected on-site vegetation, surface layers of soil, and the seed bank. The OG surfaces had many germinants comparable to those of the GB surfaces, but for diametrically opposed reasons. The OG surfaces virtually were never flooded and were, therefore, subject only to the infrequent disturbances of fire and wind characteristic of the upland forest. Other factors contributing to sparse seed banks in the OG surfaces were (1) a relatively sparse seed rain during the study year coupled with the generally short-lived nature of coniferous tree seeds (USDA Forest Service 1974), (2) the death of seeds in the seed bank because of the longevity of the forest, and (3) an absence in the on-site vegetation of early successional species, which produce many of the seeds typically found in seed banks.

Similar patterns in seed bank size and diversity have been observed in other studies in temperate forest regions (for example, Everett and Sharrow 1983, Graber and Thompson 1978, Hill and Stevens 1981, Kellman 1974, Livingston and Allessio 1968, Oosting and Humphreys 1940). Disturbed and early successional sites typically have more diverse and greater numbers of germinants than seed banks of older, more stable sites.

The seed banks of the riparian habitats we studied represented a large and rich source of propagules. A large component of species that were not represented in the vegetative state were present in the form of seeds. As with seed rain, riparian seed banks have the potential of significantly contributing to the revegetation of disturbed streamside surfaces.

Acknowledgments

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Equivalents

When you know:	Multiply by:	To find:
Centimeters (cm)	2.54	Inches
Meters (m)	3.281	Feet
Kilometers (km)	0.621	Miles
Celsius (C)	1.8 and add 32	Fahrenheit

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Harmon, Janice M.; Franklin, Jerry F. 1991. Seed rain and seed bank of third- and fifth-order streams on the western slope of the Cascade Range. Res. Pap. PNW-RP-480. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 27 p.

We compared the composition and density of the on-site vegetation, seed bank, and seed rain of three geomorphic and successional surfaces along third- and fifth-order streams on the western slope of the central Cascade Range in Oregon.

The on-site vegetation generally was dominated by tree species, the seed bank by herb species, and the seed rain by tree and herb species. Seed rain density generally corresponded to the successional stage of the geomorphic surface and frequency of site disturbance, with the youngest and least vegetatively stable geomorphic surfaces having the highest density of trapped viable seeds. The highest density and greatest species richness of seed bank germinants were found on the intermediate-aged geomorphic surfaces, which had moderate levels of disturbance. In comparison, the younger and older geomorphic surfaces (with greater and lesser disturbance levels than the intermediate-aged surfaces, respectively) had equal but lower seed bank densities. The seed banks of the youngest, least stable geomorphic surfaces, however, were substantially richer in species than those of the oldest, most vegetatively stable surfaces.

Keywords: Disturbance, riparian zones, seed bank, seed rain, species richness.

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